FACTORS AFFECTING HABITAT PREFERENCES IN THE LEPIDOPTERA

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It is well known that many species of Lepidoptera have specific habitat requirements, and that their geographic distribution, at least in part, reflects the availability of favourable habitats. Habitat favourability may depend on presence of larval or adult food resources, appropriate adult roosting sites, suitable conditions for flight and so on. However, little comparative work has been done to address several questions. Are habitat biases active or passive? Do Lepidoptera actively seek and then stay in favourable habitats, or do those in favourable habitats survive and reproduce while those in other habitats die? What factors affect habitat preferences? How strong may habitat preferences be?

Results of a single night's light trapping in 1984 suggested that in some species, preferences could be active and strong. Two Heath moth traps, operated 50 yards apart, one in a Douglas fir (*Pseudotsuga menziesii* (Mirbel)) plantation, the other in mixed deciduous woodland, produced quite different catches. For example, all *Hylaea fasciaria* were taken in the conifer plantation trap. Conversely, all *Diarsia mendica* were taken in the deciduous woodland trap. Furthermore, of polymorphic species, such as *Semiothisa liturata* and *Alcis repandata*, significant differences were found in the frequencies of forms in the two habitats (Kearns & Majerus, 1987). Other workers have found similar results in respect of a number of polymorphic species (Jones *et al.*, 1993; Aldridge *et al.*, 1993; Fraiers *et al.*, in press).

Waring (1989) has published results of a more extensive trapping run. During 1984 and 1985 he operated Heath traps one night a week in three contrasting woodland habitats in Bernwood Forest; conifer plantation, overgrown coppice broad-leaf and newly coppiced broad-leaf. Taking account of the differences of shading at trap sites, following Bowden (1982), he compared the catches of moths in overgrown coppiced broad-leaf woodland with those in conifer plantation and newly coppiced broad-leaf. Of 50 species of moth taken in sufficient numbers to allow analysis, only one, *Agriopis aurantaria* was shown to have no significant preference in either comparison for both years. More preferences were for the overgrown coppice than for the more man-managed habitats, but it is interesting to note that for each of the ten species shown to have a preference for conifer plantation, the preference was consistent between years.

Waring's data transformation, based on Bowden's formula of trapping efficiency being correlated to background illumination, is open to criticism. Recently, Dearnaley *et al.* (in prep.), have shown that the trapping efficiency of moth traps depends not only on degree of shading, but also on bulb strength, bulb height, trap design and the height of the trap above the ground. However, for many species, Waring's statistical findings are robust, even if the data are not transformed.

Waring (1989) interprets his results primarily in the light of larval foodplants and adult roosting sites. The habitat preferences shown by many, but not all, species make sense in terms of what is known about these factors. However, microclimatic factors such as temperature, humidity, windspeed etc., which may affect flight, are not considered. This may be because Waring considered that such factors would not differ significantly between his trapping sites, all being in woodland of one sort or another.

In this paper we present data obtained by running paired moth traps, within sight of each other, either side of a sharp habitat boundary between dense woodland and open grassland. The results are discussed in relation to the factors which may affect habitat specialization, including larval foodplants, roosting sites and microclimatic differences between trap sites which may affect flight.

METHODS

Trapping was carried out using paired light traps between 16 and 30 June, 1989 and between 28 June and 6 July 1990, in Juniper Bottom, Box Hill, Surrey. Juniper Bottom is an east–west running valley. The vegetation in the bottom of the valley is chalk grassland, close-cropped by rabbits, with a few standard broad-leaf trees and patches of mixed broad-leaf scrub. It is very rich in terms of number of plant species. Conversely, large areas of both sides of the valley are covered by mature yew woodland. The canopy of this woodland is extremely dense, and the under canopy is dark with virtually no ground vegetation except beneath occasional deciduous trees, such as whitebeam, and below breaks in the canopy caused by the 1987 October gales. The boundary between these yew-covered slopes and the bottom of the valley is sharply defined, consisting of a rather impenetrable natural mixed broad-leaf hedge. The site was chosen for this study because of the contrast between the habitats either side of the hedge. The extreme paucity of the ground vegetation under the yew, large parts of the yew woodland effectively being a natural monoculture, provide a sharp contrast to the species richness of the chalk grassland. A list of the identified species of plants growing within 5 m of the traps in the two habitats is given in Table 1.

Up to three pairs of traps were run on a night. Three types of trap were used; 125-W Robinson traps; 100-W 'dustbin' traps and 12-W Heath traps, both traps of a pair being the same type. Robinson and dustbin traps were powered by E650 Honda generators. Heath traps were powered by 12-V car batteries. One trap of each pair was set up approximately 10 m inside the yew woodland, the other being placed approximately 10 m outside the yew wood in the chalk grassland. In 1989, the positions of pairs of traps along Juniper Bottom varied between nights. In 1990, three pairs of trapping sites were occupied each night, the types of trap at each site varying between nights. Traps were run for 3–4 h between 9.30 p.m. and 1.30 a.m.

When trapping was terminated for a night, the traps were stoppered and transported to Juniper Hall Field Studies Centre, where the catches were scored the following morning. All macrolepidoptera were identified except the pugs (excluded due to time constraints and the inexperience of the scorers with this group).

In 1990, measurements of windspeed, temperature and humidity were taken, at each trap site, at intervals throughout the trapping period. Windspeed was measured over 10-min periods using a cup anemometer. Temperature and humidity were measured using a whirling hydrometer. Readings of light intensity at different sites in each habitat were taken using a photographic light meter.

Table 1. Plant species within five metres of (a) the traps inside the yew woodland and (b) the traps in the chalk grassland.

(a) yew, mosses, dogs mercury, whitebeam, lichens.
(b) silverweed, nettles, thistles, hawthorn, dogs mercury, hairy saint john's wort, bramble, hogweed, speedwell, bedstraws, dark mullein, marjoram, thyme, ribbed melilot, convolvulus, dead-nettle, docks, plantains, buttercups, beech, fine-leaved sandwort, mouse ear, clovers, dogwood, wood sage, hazel, beaked hawk's-beard, bugle, crosswort.

RESULTS

The total number of individuals taken in the yew woodland and the chalk grassland habitats, for each species, over the two trapping periods combined, are given in Table 2. The species are named and ordered following Skinner (1984).

Because only one anemometer was available, windspeed could only be assessed in one habitat at a time, so the two habitats could not be monitored concurrently. The data, while showing windspeed to be generally lower in the yew woodland than outside it, are not strictly comparable. However, further work in Juniper Bottom, in 1991 and 1992, using paired anemometers, has shown that the mean windspeed is markedly lower in the yew woodland than outside it (Fraiers & Cox, pers. comm.). In 1990, and subsequent years, the temperature inside the yew woodland was generally the same as, or slightly lower than, that in the grassland when trapping began each night, but declined less rapidly, so that by the end of trapping it was fairly consistently 0.5–1.5°C higher inside the yew woodland.

The background light intensity, measured during the day, was substantially higher in the grassland than in the yew, the mean ratio being 32.2:1.

ANALYSIS

For species taken in reasonable numbers (more than 10) over the 2 years, the number of moths taken inside and outside the woodland was compared using the chi-squared test (a statistical test which estimates the probability of any bias in the actual result, away from the expected result, being due to chance alone, i.e. sampling error). Initially tests were performed using the simple expectation that there was an equal probability of a moth being caught in either habitat: i.e. an expected ratio of 0.5:0.5 for a species in the two habitats. The normal level of statistical significance, that there is less than a 5% probability of any deviation in the observed data away from expectation being due to chance sampling error alone, is used. The results of these analyses are given in Table 3.

Of course, these tests may be unreliable were traps in one habitat much more efficient in attracting and catching macrolepidoptera than those in the other habitat. The total number of moths of all species recorded in each habitat (1624 in the yew wood, 883 in the grassland) show that this might be the case. One method of circumventing this problem would be to bias the chi-squared expectations by the ratio of total moths captured in each type of habitat. This would give an expectation ratio of 0.648:0.352. The results of repeating the chi-squared tests with these transformed expectations are also given in Table 3.

This statistical recourse could also be criticized because the greater number of moths taken in the yew woodland traps, compared to the grassland traps, is primarily a consequence of four common species, *Idaea aversata*, *Peribatodes rhomboidaria*, *A. repandata* and *Campaea margaritata*, which all show significant bias towards the yew woodland, with either expectation ratio. If the data for these four species are removed from the catch totals for each habitat, these are reduced to 699 for yew woodland and 652 for chalk grassland.

It is notable that there is general tendency for geometrid species to be taken in larger numbers in the yew woodland and noctuid species to be taken in larger numbers in the grassland. This may result from differences in windspeed in the two habitats. The windspeed in woodland is generally lower than in open habitats. This has been confirmed for the two habitats in question. The yew woodland may thus provide sheltered conditions that would be more conducive to flight for

Table 2. Total number of moths caught in yew woodland and chalk grassland. The class of build of each species used in statistical analysis (see text) is given: D = delicate, R = robust, ? = uncertain.

Species	Build	In yew wood	In grassland	Total
Hepialus lupulinus L.	?	0	1	1
Drepana falcataria L.	D	0	2	2
Thyatira batis L.	R	4	5	9
Habrosyne pyritoides Hufn.	R	1	4	5
Ochropacha duplaris L.	R	3	1	4
Hemithea aestivaria Hübn.	D	6	4	10
Cyclophora linearia Hübn.	D	7	16	23
Timandra griseata Petersen	D	3	0	3
Idaea biselata Hufn.	D	18	3	21
Idaea dimidiata Hufn.	D	3	1	4
Idaea trigeminata Haw.	D	2	3	5
Idaea aversata L.	D	103	33	136
Xanthorhoe fluctuata L.	D	2	0	2
Scotopteryx bipunctaria D. & S.	D	2	0	2
Epirrhoe alternata Müller	D	0	1	1
Epirrhoe rivata Hübn.	D	0	2	2
Camptogramma bilineata L.	D	3	0	3
Cosmorhoe ocellata L.	D	11	2	13
Ecliptopera silaceata D. & S.	D	0	1	1
Chloroclysta truncata Hufn.	D	10	11	21
Cidaria fulvata Forster	D	4	4	8
Plemyria rubiginata D. & S.	D	5	1	6
Thera obeliscata Hübn.	D	14	6	20
Thera sp.	D	2	0	2
Electrophaes corylata Thunb.	D	0	1	1
Colostygia pectinataria Knoch	D	14	27	41
Hydriomena furcata Thunb.	D	9	14	23
Horisme vitalbata D. & S.	D	1	0	1
Horisme tersata D. & S.	D	28	14	42
Melanthia procellata D. & S.	D	6	8	14
Philereme vetulata D. & S.	D	5	6	11
Philereme transversata Hufn.	D	4	1	5
Perizoma flavofasciata Thunb.	D	1	0	1
Hydrelia flammeolaria Hufn.	D	4	0	4
Lomaspilis marginata L.	D	2	3	5
Ligdia adustata D. & S.	D	1	1	2
Semiothisa notata L.	D	1	0	1
Semiothisa liturata Clerck	D	18	8	26
Plagodis dolabraria L.	D	3	0	3
Opisthograptis luteolata L.	D	18	5	23
Crocallis elinguaria L.	?	5	2	7
Ourapteryx sambucaria L.	D	12	1	13
Biston betularia L.	?	4	4	8
Peribatodes rhomboidaria D. & S.	D	223	64	287
Deileptenia ribeata Clerck	D	11	0	11
Alcis repandata L.	D	527	117	644
Boarmia robararia D. & S.	D	1	0	1
Serraca punctinalis Scop.	D	0	1	1
Ectropis bistortata Goeze	D	11	1	12
Ectropis crepuscularia D. & S.	D	10	6	16
Paradarisa extersaria Hübn.	D	2	0	2
Cabera pusaria L.	D	16	5	21
Cabera exanthemata Scop.	D	9	2	11
Lomographa temerata D. & S.	D	1	4	5
Campaea margaritata L.	D	72	17	89
Hylaea fasciaria L.	D	11	3	14
Sphinx ligustri L.	R	3	8	11
Hyloicus pinastri L.	R	1	3	4
Phalera bucephala L.	R	0	1	1
Stauropus fagi L.	R	3	6	9
Notodonta dromedarius L.	R	0	1	1
Pheosia gnoma F.	R	1	1	2
Ptilodon capucina L.	R	3	1	4

Table 3. Chi-squared analysis comparing the number of moths of each species in yew wood-
land and chalk grassland. Criterion for inclusion: more than 10 moths taken. Two series
of tests using different expected ratios are given. In the first (A) the expected likelihoods
of a moth being caught in either habitat are equal. In the second (B) the probability of
being caught in a particular habitat is weighted by the number of all moths caught in that
habitat as a proportion of all moths in both habitats i.e. 0.648 for yew woodland, and 0.352
for chalk grassland. The direction of significant biases are given, with probability confidence limits
(ns means non-significant, i.e. the bias could be due to chance sampling error. Degrees of freedom = 1
throughout).

Species	Chi-squared (χ^2) analysis	
	A χ^2; p; bias	B χ^2; p; bias
Hemithea aestivaria	ns	ns
Cyclophora linearia	ns	11.89; <0.001; grass
Idaea biselata	10.71; <0.005; yew	4.04; <0.05; yew
Idaea aversata	36.03; <0.001; yew	7.13; <0.01; yew
Cosmorhoe ocellata	6.23; <0.05; yew	ns
Chloroclysta truncata	ns	ns
Thera obeliscata	ns	ns
Colostygia pectinataria	4.12; <0.05; grass	17.0; <0.001; grass
Hydriomena furcata	ns	6.64; <0.01; grass
Horisme tersata	4.67; <0.05; yew	ns
Melanthia procellata	ns	ns
Philereme vetulata	ns	ns
Semiothisa liturata	3.85; <0.05; yew	ns
Opisthograptis luteolata	7.35; <0.01; yew	ns
Ourapteryx sambucaria	9.31; <0.005; yew	4.18; <0.05; yew
Peribatodes rhomboidaria	88.09; <0.001; yew	20.9; <0.001; yew
Deileptenia ribeata	11.00; <0.001; yew	5.40*; <0.05; yew
Alcis repandata	261.02; <0.001; yew	81.80; <0.001; yew
Ectropis bistortata	8.33; <0.005; yew	ns
Ectropis crepuscularia	ns	ns
Cabera pusaria	5.76; <0.05; yew	ns
Cabera exanthemata	4.45; <0.05; yew	ns
Campaea margaritata	33.99; <0.001; yew	10.11; <0.005; yew
Hylaea fasciaria	4.57; <0.05; yew	ns
Agrotis clavis	ns	6.51; <0.01; grass
Agrotis exclamationis	4.61; <0.05; grass	39.56; <0.001; grass
Axylia putris	ns	ns
Ochropleura plecta	4.57; <0.05; yew	ns
Noctua pronuba	ns	ns
Anaplectoides prasina	ns	ns
Hada nana	ns	ns
Mythimna pallens	9.78; <0.005; grass	22.64; <0.001; grass
Rusina ferruginea	7.14; <0.01; grass	15.67; <0.001; grass
Apamea monoglypha	ns	ns
Apamea sublustris	ns	10.49; <0.005; grass
Oligia spp.	ns	3.94; <0.05; grass
Caradrina morpheus	ns	5.19; <0.05; grass
Lithacodia pygarga	7.12; <0.01; grass	16.60; <0.001; grass
Diachrysia chrysitis	ns	5.41*; <0.05; grass
Autographa pulchrina	ns	15.67; <0.001; grass
Abrostola triplasia	8.33; <0.005; yew	ns
Laspeyria flexula	ns	ns
Rivula sericealis	ns	7.80; <0.01; grass
Hypena proboscidalis	11.65; <0.001; yew	ns
Pechipogo strigilata	11.00; <0.001; yew	5.40*; <0.05; yew
Herminia nemoralis	8.07; <0.005; yew	ns

*Yates' correction used for low expected values.

Table 4. Comparison of numbers of 'delicate' compared to 'robust' moths taken in yew woodland and chalk grassland. Only data from those species which did not give a significant result in the analyses given in Table 3 are included.

	Yew Woodland	Chalk Grassland	Totals
Delicate	129	85	214
Robust	149	194	342
Totals	277	279	556

Heterogeneity Chi-squared = 15.24; d.f. = 1; $P < 0.001$.

light-bodied, large-wing-area species, as characterized by the geometrids. On the other hand, for the more robust build characteristic of many noctuids, shelter from wind may not be of such great importance. Of course, not all geometrids are 'delicate' and not all noctuids 'robust'. To consider this further, all species were categorized as either delicate (D) or robust (R). The categories are given in Table 2. In a small number of cases the category that a species should be placed in was not obvious, and these species have been omitted from the analysis. The number of moths of species which showed no significant bias to either habitat in either of the analyses given in Table 3, and all those taken that were not analysed due to insufficient numbers taken, were totalled under the assigned classes D and R for each habitat. The results are given in Table 4. A heterogeneity chi-squared test, comparing the ratios of the classes between the two habitats shows that overall the 'delicate' species are taken in significantly higher numbers in the yew woodland than the grassland, the reverse being the case for the 'robust' species.

DISCUSSION

Consideration of the species taken in large enough numbers for individual analysis, suggests that, with some exceptions, those species with large wing area to body weight ratios, i.e. the more delicate species, tend to be caught more commonly inside the yew woodland than in the grassland. The reverse is true for the more robust species. These deductions are endorsed by the general comparison between delicate and robust moths (Table 4). One interpretation of these findings is that delicate, less strongly flying species may habitually seek shelter from the wind in dense woodland such as the yew woodland in this study. However, that is not to say avoidance of wind buffeting is the only factor producing the biases observed, and it is pertinent to consider each species, showing a significant bias to one habitat or the other, individually. This is done in Table 5 in which, for each of the relevant species, the type of habitat bias, whether they are classed as delicate or robust, their larval food plant, their roosting behaviour, and a tentative deduction of the principal factor influencing the habitat bias they show, is given.

In the majority of cases seemingly sensible reasons for the habitat preferences observed can be given. In some cases, such as *P. rhomboidaria*, *Deileptenia ribeata* and *A. repandata* it is probable that all three factors under consideration contribute to the behaviour. For the majority of the 'delicate' species, using the yew woodland as a sheltered flight corridor is probably the principal cause of the observations, and in many cases over-rides larval foodplant. There are three species which buck this trend. It is possible that in each of the three, *Cyclophora linearia*, *Colostygia pectinataria* and *Hydriomena furcata*, proximity to larval foodplants takes precedence. This is almost certain in the case of *C. linearia*, for it was taken most often in a trap

Table 5. The habitat bias, build, larval foodplant and roosting sites for each of the species showing a statistically significant habitat bias. The most important factor determining this bias is tentatively proposed for each species.

Species	Habitat bias	Build	Larval food	Roosting sites	Principal factor
C. linearia	G	D	Beech	Foliage	Fdpt.
I. biselata	Y	D	Various plants	Foliage	Sh. fl.
I. aversata	Y	D	Various low plants	Foliage	Sh. fl.
C. ocellata	Y	D	Bedstraws	Foliage	Sh. fl.
C. pectinataria	G	D	Bedstraws	Foliage	? Fdpt.
H. furcata	G	D	Sallows, various bushes	Bark and foliage	? Fdpt.
H. tersata	Y	D	Traveller's joy	? Foliage	Sh. fl.
S. liturata	Y	D	Needled conifers	Bark, conifer foliage	Fdpt.
O. luteolata	Y	D	Various broad-leaf trees	Foliage	Sh. fl.
O. sambucaria	Y	D	Various trees, shrubs	Foliage	Sh. fl.
P. rhomboidaria	Y	D	Various trees inc. yew	Bark	Fdpt., roost, Sh. fl.
D. ribeata	Y	D	Various trees inc. yew	Bark	Fdpt., roost, Sh. fl.
A. repandata	Y	D	Various trees inc. yew	Bark	Fdpt., roost, Sh. fl.
E. bistortata	Y	D	Various broad-leaf trees	Bark	Roost, Sh. fl.
C. pusaria	Y	D	Various broad-leaf trees	Foliage	Sh. fl.
C. exanthemata	Y	D	Sallows, aspen	Foliage of foodplant	Sh. fl.
C. margaritata	Y	D	Various broad-leaf trees	Foliage	Sh. fl.
H. fasciaria	Y	D	Needled conifers	Bark, conifer foliage	Fdpt., roost, Sh. fl.
A. clavis	G	R	Various low plants	Low vegetation, litter	Fdpt., roost
A. exclamationis	G	R	Various low plants	Low vegetation, litter	Fdpt., roost
O. plecta	Y	R	Various low plants	Low vegetation	?
M. pallens	G	R	Various grasses	Low vegetation	Fdpt., roost
R. ferruginea	G	R	Various low plants	Unknown	? Fdpt.
A. sublustris	G	R	? Various grasses	Low vegetation	Roost, ? Fdpt.
Oligia spp.	G	R	Various grasses	Bark, low vegetation	Fdpt.
C. morpheus	G	R	Low growing plants	Low vegetation, litter	Fdpt., roost
L. pygarga	G	R	Various grasses	Unknown	Fdpt.
D. chrysitis	G	R	Low growing plants	Low vegetation	Fdpt., roost
A. pulchrina	G	R	Various low plants	Vegetation	Fdpt., roost
A. triplasia	Y	R	Nettle	? Bark, foliage	? Roost
R. sericealis	G	?	Various grasses	Low vegetation	Fdpt., roost
H. proboscidalis	Y	D	Nettle	Bark, foliage, low vegetation	Sh. fl.
P. strigilata	Y	D	? Withered broad-leaf leaves	Bark, foliage	Sh. fl.
H. nemoralis	Y	D	Oak, alder	Bark foliage	Sh. fl.

Abbreviations: G grass, Y yew, D delicate, R robust, Fdpt. foodplant, Sh. fl. sheltered flight.

on the chalk grassland adjacent to a mature beech and larch plantation. For the other two species, although their larval foodplants grow closer to the grassland traps than the yew traps, the same could be said of many of the other 'delicate' species, and it is not so obvious why these two species buck the trend.

Among the robust species, the need for a sheltered flight corridor would not be expected to be an important factor contributing to flight behaviour. In these species, larval foodplants and roosting sites take precedence, and as none of the species feeds on yew, the expectation is that these species should be trapped most frequently in the grassland habitat. In the majority of cases where a bias is seen, this is the case, but again there are exceptions, both *Ochropleura plecta* and *Abrostola triplasia* apparently preferring the woodland habitat. In the latter species, finding a roosting site may be a contributing factor, but this suggestion is very tentative. For *O. plecta*, no convincing case can be made on the basis of any of the factors under consideration.

The results contained herein broadly endorse Waring's (1989) findings that many species of moth show habitat flight preferences. They suggest that for geometrid-like species, but not for the more robust noctuid-like species, dense woodland may provide a sheltered flight corridor, a factor alluded to by Waring in respect of *Idaea biselata* and *I. aversata*. In the majority of cases, a sensible interpretation of the habitat biases seen, based on current knowledge of the species in question, can be made.

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